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Inferring extinctions from sighting records of variable reliability

Tamsin E. Lee[1]*, Michael A. McCarthy[1], Brendan A. Wintle[1], Michael Bode[1], David L. Roberts[2] and Mark A. Burgman[1]

[1]*School of Botany, University of Melbourne, Parkville 3010, Australia; and* [2]*Durrell Institute of Conservation and Ecology, School of Anthropology and Conservation, University of Kent, Kent CT2 7NR, UK*

Summary

1. A range of mathematical models has been developed to infer whether a species is extinct based on a sighting record. Although observations have variable reliability, current methods for detecting extinction do not differentiate observation qualities.

2. A more suitable approach would consider certain and uncertain sightings throughout the sighting period. We consider a small population system, meaning we assume sighting rates are constant and the population is not declining. Based on such an assumption, we develop a Bayesian method that assumes that certain and uncertain sightings occur independently and at uniform rates. These two types of sightings are connected by a common extinction date. Several rates of false sightings can be calculated to differentiate between observation types. Prior rates of false and true sightings, as well as a prior probability that the species is extant, are included. The model is implemented in OpenBugs, which uses Markov chain Monte Carlo (MCMC).

3. Based on records of variable reliability, we estimate the probability that the following species are extinct: Caribbean seal *Monachus tropicalis,* grey, black-footed ferret *Mustela nigripes,* Audubon & Bachman, greater stick-nest rat *Leporillus conditor,* Sturt, and lesser stick-nest rat *Leporillus apicalis,* Gould. As further examples, Birdlife International provided the sighting records for the Alaotra grebe *Tachybaptus rufolavatus,* Delacour, Jamaica petrel *Pterodroma caribbaea,* Carte, and Pohnpei mountain starling *Aplonis pelzelni,* Finsch, with prior probabilities for extinction. The results are compared with existing methods, which ignore uncertain sightings. We find that including uncertain sightings can considerably change the probability that the species is extant, in either direction. However, in our examples, including the quality of the uncertain sighting made little difference. When we ignore uncertain sightings, our results agree with existing methods, especially when the last sighting was near the end of the sighting period.

4. *Synthesis and applications*. Estimating the probability that a species is extinct based on sighting records is important when determining conservation priorities and allocating available resources into management activities. Having a model that allows for certain and uncertain observations throughout the sighting period better accommodates the realities of sighting quality, providing a more reliable basis for decision-making.

Key-words: anomalous reports, Bayes factor, extirpation, species persistence, uncertainty

Introduction

Inferring whether a species is extinct is of interest to ecologists from a variety of fields. Knowing the probability that a species is extinct allows informed decisions to be made about investing time and money into its preservation and carrying out surveys. On a broad scale, extinction rates are used to measure biodiversity conservation effectiveness [May, Lawton & Stork (1995), Commonwealth of Australia (1996), Flannery & Schouten (2001) and IUCN (2002)]. Ideally, field studies would be rigorous and without uncertainty. Nonetheless, false-positive errors arise when a species is mistakenly recorded, and false negatives arise when observers fail to note a species. Incorrectly classing a species as extinct or extant can lead to failure to conserve a threatened species,

*Correspondence author. E-mail: tamsin.lee@unimelb.edu.au

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wasted conservation effort directed towards a species that are mistakenly thought to persist or erosion of public confidence when a species reappears after being classified as extinct (the Lazarus effect; Keith & Burgman 2004; Roberts & Kitchener 2006). Extinctions of particular species are rarely observed directly and, in many cases, can only be inferred from sighting or collection records. Solow & Roberts (2003). Solow (1993a), Burgman, Grimson & Ferson (1995), McCarthy (1997), Rout, Salomon & McCarthy (2009) and Solow *et al.* (2011) developed and applied mathematical models to indicate whether a species is extinct based on a list of time intervals (usually years) in which the species was sighted.

Models that infer extinction from a sighting record typically ignore the possibility of false positives by either ignoring uncertain sightings or classing them as certain sightings. Without a formal approach to account for uncertain sightings, problems may emerge when making decisions about the conservation of a species. For example, the debate about the extinction of the ivory-billed woodpecker largely revolves around questions of false or true-positive sightings. Since uncertain sightings have occurred as recently as 2004, the US Fish and Wildlife service has drafted a multimillion dollar recovery plan for this species (Decision Point 2012).

Solow *et al.* (2011) included the possibility of false positives when inferring extinction from a sighting record. Accounting for false sightings means that sightings occur after extinction; however, the sightings occur at a different rate. Suppose extinction occurs at time T_E, and recall that we assume sighting rates are constant and the small population is not declining. Then, the rate of sightings before extinction (at time T_E) is different to the rate after extinction, making T_E a change point. Inferring where this change point occurs gives the time of extinction. The method of Solow *et al.* (2011) takes an approach similar to the work of Raftery & Akman (1986), where a change point is included in the Bayesian analysis of a Poisson's process. Raftery & Akman (1986) do not apply their method to infer extinction from a sighting data. However, their method can be used such that there are two (true and false) constant sighting rates that predict the change point T_E. Where Raftery & Akman (1986) consider only one change point (T_E), Solow *et al.* (2011) divide the sighting period into three (see Figs 1b–c). This is consistent with the ivory-billed woodpecker data where uncertain sightings occur after an initial period of certain sightings (Roberts, Elphick & Reed 2009). Solow *et al.* (2011) also assumed two constant sighting rates (true and false). These sighting rates are assumed constant, and uncertain sightings are only introduced after time t_L.

While the method of Solow *et al.* (2011) is suitable for some data sets, in general, uncertain sightings arise throughout the observation period. We build on the work of Solow *et al.* (2011) to account for the fact that some sightings will be more certain than others. For example, records based on specimens are largely certain, while photographs and field observations without specimens are less certain to be true positives (Roberts & McInerny 2003). In this circumstance, we can think of two concurrent sighting records. One, based on specimens, might be assumed to be largely free of false positives, while a second sighting record, based on field observations, might be prone to false positives. Of course, there may be more than one kind of uncertain record (e.g. photographs, expert visual records and audio records). Uncertain sightings of an endangered species are especially prone to external factors, for example the publicity arising from a certain sighting record. By assuming certain and uncertain sightings are independent, we are ignoring such factors.

Here, a model is developed to incorporate both certain and uncertain sightings throughout the sighting period (see

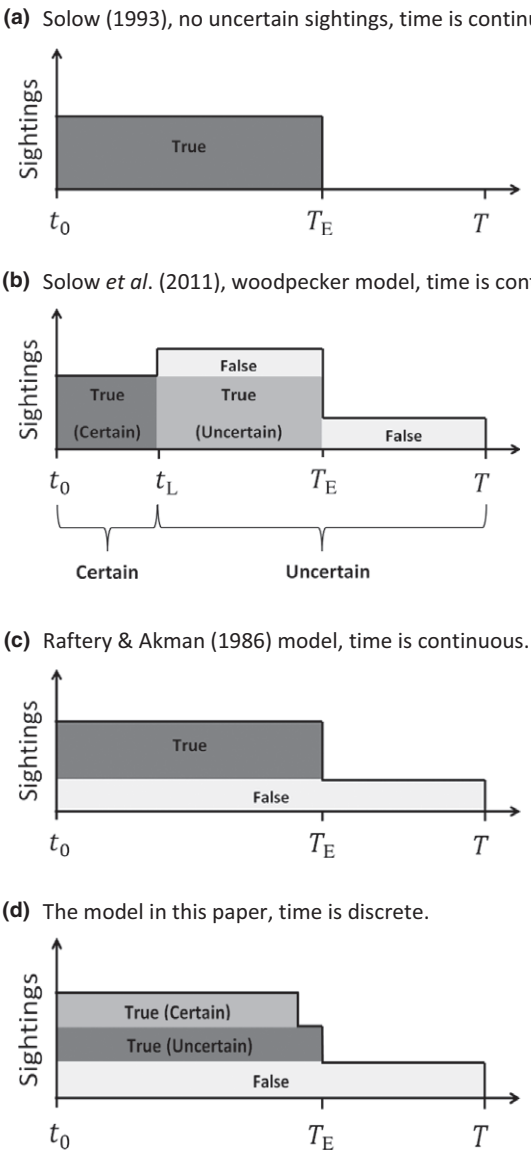

Fig. 1. Representations of assumed sighting records for various models.

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Fig. 1d). Furthermore, we assume that certain sightings and uncertain sightings that are true (valid) occur at different rates, whereas Solow *et al.* (2011) assumed that these two types of true sightings occur at the same rate. For the case where certain sightings are not incorporated, the method resembles the work of Solow (1993a). Where certain sighting records are absent, our method resembles the work of Raftery & Akman (1986). Solow (1993a) and Solow *et al.* (2011) were based on continuous time with the times of all sightings known. The method here uses discrete uniform time intervals, such as years, and does not allow for multiple sightings in one time interval. To include such multiple sightings, the time interval can be smaller, where a very small time interval converges to the continuous case. However, the smaller the time interval, the more extensive the computation time. In reality, most sighting records have a discrete resolution, for example annual (Solow 2005). Considering years as time intervals corresponds to sighting records from Burgman, Grimson & Ferson (1995), where the sighting record simply lists the years in which the species was seen. The method presented here is applied to these sighting records later in this paper.

The next section presents the method in detail. Since our method is an extension of Solow (1993a) (but discrete), we also briefly describe the method of Solow (1993a). In the case of no false sightings, results from our method are compared with results from the method of Solow (1993a).

Materials and methods

The sighting record for a potentially extinct species is described with vector

$$\underline{s} = (s_1, s_2, s_3, \ldots, s_j, \ldots, s_{\tilde{N}}),\ s_j = \{0, 1\}, \qquad \text{eqn 1}$$

where all sightings occurred during a finite observation period (0, T). Each entry represents a consistent time interval. Each s_j is either 0 for no sighting or 1 when the species is sighted at least once in the time interval. We assume each sighting is independent. For simplicity, we consider the case where each time interval represents a year, such that $\tilde{N} = T$.

Consider the null hypothesis that extinction has not occurred, H_0, against the alternative hypothesis that it has, H_1. For a specified prior probability that the species is extant π, the Bayesian probability that the species is extant H_0 is defined as

$$P(H_0|\underline{s}) = \frac{l(\underline{s}|H_0)\pi}{l(\underline{s}|H_0)\pi + l(\underline{s}|H_1)(1-\pi)}.$$

This is commonly written in the form

$$P(H_0|\underline{s}) = \left(1 + \frac{1-\pi}{\pi B(\underline{s})}\right)^{-1}, \qquad \text{eqn 2}$$

where B(s) is the Bayes factor defined as a ratio of the likelihoods

$$B(\underline{s}) = \frac{l(\underline{s}|H_0)}{l(\underline{s}|H_1)}. \qquad \text{eqn 3}$$

Determining these likelihoods is not straightforward and may involve integrals without an upper limit (indefinite integrals) making them a challenge to evaluate. Solow (1993a) overcomes problems with the indefinite integral limit by assuming that sightings follow a Poisson's distribution with constant sighting rate until extinction. For his model, Solow (1993a) considers all the sightings to be true, meaning that after extinction there are no sightings (Fig. 1a). The Bayes factor (eqn 3) can then be simplified to

$$B(\underline{s}) = \frac{S-1}{(T/t_n)^{S-1} - 1}, \qquad \text{eqn 4}$$

where S is the total number of sightings and t_n is the time of the last sighting. Hereafter, eqn 4 is referred to as 'Solow's 1993 equation'. Burgman, Grimson & Ferson (1995), Roberts & McInerny (2003), McInerny *et al.* (2006), Roberts & Kitchener (2006), Rout, Salomon & McCarthy (2009), Vogel *et al.* (2009) and Elphick, Roberts & Reed (2010) have used Solow's 1993 equation to infer extinction.

Our approach differs to Solow's 1993 equation because we state that sightings may be true or false, so sightings may occur after extinction. The constant sighting rates are m_c for a certain sighting such as a specimen, m_u for an uncertain sighting that is a true sighting and f for a false positive (an uncertain sighting that is in fact a false sighting). The simplest case would be the one considered by Solow (1993a) where there are no false sightings, $f = 0$. A more realistic scenario would have a sighting record that is composed of both false positives and true positives.

We consider two sets of sighting data, where one records certain sightings only $\underline{s}_c$, and the other records uncertain sightings only $\underline{s}_u$. These sighting records have a common time to extinction, but the occurrence of certain and uncertain sightings is independent. As previously mentioned, Solow (1993a) assumed that sightings follow a stationary Poisson's process. Similar assumptions are made here: the number of certain records follow a Poisson's distribution with constant mean m_c before the time of extinction T_E, and zero after T_E; and the number of uncertain records follow a Poisson's distribution with constant mean $m_u + f$ before T_E, and f after T_E. A Poisson's distribution states that $P(\text{event} = 0) = \exp(-\text{mean})$. Hence, at time i ($i$ = 1,…,T_E,…, T) at least one certain observation would occur with probability

$$P(\text{certain observation}_i) = \begin{cases} 1 - e^{-m_c} & i < T_E, \\ 0 & i \geq T_E, \end{cases} \qquad \text{eqn 5}$$

and one uncertain probability would occur with probability

$$P(\text{uncertain observation}_i) = \begin{cases} 1 - e^{-(m_u+f)} & i < T_E, \\ 1 - e^{-f} & i \geq T_E, \end{cases} \qquad \text{eqn 6}$$

The likelihood of the data under H_0 (extant) is

$$l(\underline{s}|H_0) = l(\underline{s}_c|H_0)\, l(\underline{s}_u|H_0) \qquad \text{eqn 7}$$

where $l(\underline{s}_c|H_0)$ is the likelihood of the certain sighting record $\underline{s}_c$ under H_0, and $l(\underline{s}_u|H_0)$ is the likelihood of the uncertain sighting

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record $\underline{s}_u$ under H_0. The likelihood of the data under H_1 (extinct) is

$$l(\underline{s}|H_1) = l(\underline{s}_c|H_1)l(\underline{s}_u|H_1), \quad \text{eqn 8}$$

where $l(\underline{s}_c|H_1)$ is the likelihood of the certain sighting record $\underline{s}_c$ under H_1, and $l(\underline{s}_u|H_1)$ is the likelihood of the uncertain sighting record $\underline{s}_u$ under H_1. In the case of certain sightings only,

$$l(\underline{s}|H_0) = \int_0^\infty \prod_{i=0}^{\tilde{N}} (1 - e^{-m_c})^{s_i} (e^{-m_c})^{1-s_i} \mathrm{d}P(m_c).$$

For constant sighting rate m_c, s_i is not a function of time. Therefore,

$$l(\underline{s}|H_0) = \int_0^\infty (1 - e^{-m_c})^{S_c} (e^{-m_c})^{T-S_c} \mathrm{d}P(m_c), \quad \text{eqn 9}$$

where $\tilde{N} = T$, S_c is the total number of certain sightings and $P(m_c)$ is the prior distribution function of this rate. Under the hypothesis that extinction occurs, we consider the time t_n from the last certain sighting. The likelihood of extinction occurring at time T_E is the likelihood of the data given extinction occurring at a time between t_n and T, say t_E, that is,

$$\begin{aligned} l(\underline{s}|H_1) &= \int_{t_n}^{T} l(\underline{s}|T_E = t_E) \mathrm{d}P(t_E) \\ &= \int_{t_n}^{T} \int_0^\infty (1 - e^{-m_c})^{S} (e^{-m_c})^{t_E - S} \mathrm{d}P(m_c) \mathrm{d}P(t_E), \end{aligned} \quad \text{eqn 10}$$

where $P(t_E)$ is the prior distribution function of the extinction time, and the sighting rate m_c is constant. In the absence of specific prior knowledge, it is reasonable to let

$$\mathrm{d}P(m_c) = \frac{\mathrm{d}m_c}{M} \quad 0 \le m_c \le M, \quad \text{eqn 11}$$

$$\mathrm{d}P(t_E) = \frac{\mathrm{d}t_E}{T} \quad 0 \le t_E \le T, \quad \text{eqn 12}$$

where M is a finite number. The constant sighting rates are unknown, so eqn 11 assumes every value between 0 and M are equally likely to be the sighting rate. To ensure a wide range of values are considered, M should be large. Under this choice for $P(t_E)$, all values of T_E in the observation period are considered equally likely. Substituting eqns 11-12 into eqn 9 and eqn 10 gives the likelihoods for certain sightings only. In the case of certain and uncertain sighting records, the likelihood estimates (eqns 7-8) are estimated using Markov chain Monte Carlo (MCMC) analyses implemented in OpenBugs (OpenBugs, 2012). We obtain estimates for T_E, m_c, m_u and f to determine a probability that the species is extinct. The code is provided in Appendix S1 in Supporting Information. Solow used the standard noninformative prior distribution for the rate of a Poisson's process, $0 \le m_c \le \infty$. Although this distribution is improper, this posed no problems for the Bayesian approach, which simplified the Bayes factor eqn 3 to the analytic solution, Solow's 1993 equation (eqn 4). However, we choose large, finite, upper bounds on the independent sighting rates m_c, m_c and f. We assume every value between 0 and the upper bounds are equally likely to be the sighting rate. The sighting rate for certain sightings (m_c) and the rate for uncertain sightings ($m_c + f$ before T_E and f after T_E) are calculated from the prior and sighting records. At each iteration, the rate is used within a Poisson's distribution to update the probability that the species is extant.

CHOOSING A PRIOR FOR THE RATE OF FALSE-POSITIVE SIGHTINGS

When an uncertain sighting has occurred, there may be an expert judgment on the probability that this observation is a true positive. As a guide, Birdlife International has provided a table of various observation types with the corresponding suggested probabilities that these are true sightings (under the assumption the sighting occurred before extinction), see (Table 1). Let α correspond to a type of uncertain observation, such as a photograph or sound recording. Suppose $R_\alpha = P(\text{true}|\text{uncertain obs.}_\alpha)$ is provided by expert judgment. Then $P(\text{false}|\text{uncertain obs.}_\alpha) = 1 - R_\alpha$. By the definition of conditional probability,

$$R_\propto = \frac{P(\text{uncertain and true obs.}_\propto)}{P(\text{uncertain obs.}_\propto)} = \frac{1 - e^{-m_u}}{1 - e^{-(m_u + f)}} \quad \text{eqn 13}$$

Rearranging eqn 13 to make f the subject gives a prior for the rate of false sightings. Hence, instead of taking choosing f to range between 0 and a large finite number as before, we take

$$f_{\text{prior}} = -\ln\left(1 - \frac{1 - e^{m_u}}{R_\propto}\right) - m_u \text{ where } m_u \le -\ln(1 - R_\propto).$$

Notice that the rate of true uncertain sightings m_u has an upper bound, which depends on the probability that a sighting is true, R_α. A high probability that the sighting is true $R_\alpha \approx 1$ implies a larger upper bound for m_u, compared with small R_α. A further progression of the model is to differentiate uncertain sightings between photographs, observations by experts, etc., with corresponding false-positive detection rates f_1, f_2, etc. In the

Table 1. Suggested probabilities that a particular observation is a true-positive sighting, R_α

Probability observation	Observation type
0·90–0·94	Photograph or sound.
0·8–0·9	Record described as being based on collected individual.
0·6–0·8	Record based on observation described in the literature as 'confirmed' or considered fairly convincing.
0·4–0·8	Record based on observation (with no qualification in the literature or with no additional information upon which to judge veracity).
0·1–0·4	Record described in the literature as (or judged to be) unconfirmed or questionable.
0·1–0·3	Local report.

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absence of information about various observation types, it is reasonable to differentiate between true-positive sightings and false-positive sightings only.

The next section uses the definitions for the probability of a certain observation (eqn 5), and probability of an uncertain observation (eqn 6), within a MCMC framework to derive a probability that the species is extant, given the sighting records. The results are compared with the probability that a species is extant, given a certain sighting record, defined by Solow's 1993 equation (eqn 4) in eqn 2. We also present results from our analytic approach from using eqns 9-10 in eqn 3.

Results

Initially, to compare our method with Solow's 1993 equation for the Bayes factor, we consider the case of the true sightings only. For the case of certain sightings only, the Bayes factor of our method can be approximated analytically using

$$B(\underline{s}) = \frac{l(\underline{s}|H_0)}{l(\underline{s}|H_1)} = \frac{\frac{1}{M}\int_0^M (1-e^{-m_c})^S (e^{-m_c})^{T-S} \mathrm{d}m_c}{\frac{1}{MT}\int_{t_n}^T (1-e^{-m_c})^S (e^{-m_c})^{t_E-S} \mathrm{d}m_c \mathrm{d}t_E} \qquad \text{eqn 14}$$

from eqns 9-10. Hence, MCMC analyses are not necessary. We compare results from eqn 14 with results from Solow's 1993 equation,

$$B(\underline{s}) = \frac{S-1}{(T/t_n)^{S-1}-1},$$

(repeated here for convenience). The probability that the species is extant is then given by eqn 2, again, repeated here for convenience,

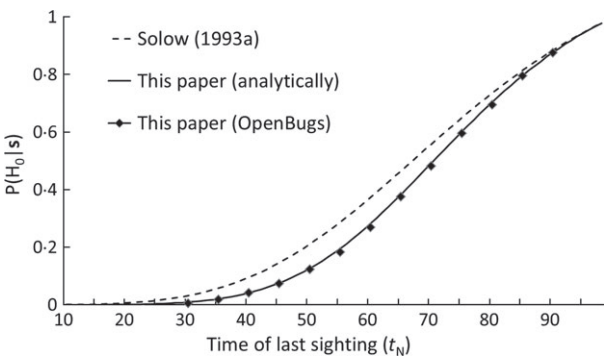
$$P(H_0|\underline{s}) = \left(1 + \frac{1-\pi}{\pi B(\underline{s})}\right)^{-1}.$$

Taking a time interval (0,100) with number of sightings $S = 5$ and prior $\pi = 0{\cdot}5$, the time of the last sighting t_n varies from 10 to 90. The results from eqn 14 and Solow's 1993 equation, along with corresponding results from MCMC analyses are plotted in Fig. 2(a). Solow's 1993 equation and our method initially appear similar. However, when the ratio t_n/T is small, the relative difference between the two methods is substantial, see Fig. 2(b). This difference arises from the different choice of $P(m_c)$.

Solow's 1993 equation and our approach were applied to sighting data presented in Burgman, Grimson & Ferson (1995), Table 2, which contains only sightings that are assumed to be true. The final time was taken to be 2011, and the prior probability of extinction π was assumed to be 0·5 (since no other prior was provided). The results are shown in Fig. 3. To apply the method to data with uncertain sightings, Birdlife International provided the data in Table 3. The values for the probability that an observation is a true-positive R_α was determined by considering the type and quality of evidence, similarity of the individual recorded to taxa with which it could potentially be confused, likely abundance of the recorded individual compared with such taxa, circumstances of the record and the skill and experience of the recorder. The three Birdlife International examples were used to compare the different approaches and sensitivity to the prior. We used the different sighting records with π as given in the table and $\pi = 0{\cdot}5$ in four ways: (i) Solow's equation using only observations with $R_\alpha = 1$ (certain sightings only); (ii) our approach using only observations with $R_\alpha = 1$ (certain sightings only); (iii) our approach where observations with $R_\alpha < 1$ were used to determine a single false sighting rate f; (iv) our approach where observations with $R_\alpha < 1$ were grouped into similar categories to determine several false sighting rates. The results are shown in Fig. 4.

In both Figs 3 and 4, the comparison with Solow's 1993 equation, and our approach with certain sightings only, is consistent with Fig. 2(b): when no false sightings are included, the two approaches give very similar results as $t_n/T \to 1$. When uncertain sightings are considered (Fig. 4), the estimate for the probability that a species is extant diverges from the results of Solow's 1993 equation, irrespective of the prior. In fact, the choice of prior does not affect the relationship of the different approaches to

(a) Comparing the probability that species is extant.



(b) Examining the difference between Solow's method and our method.

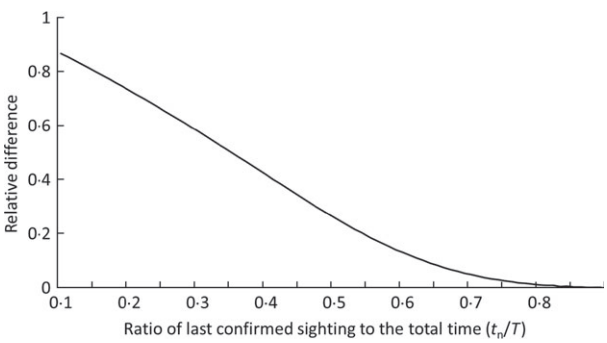


Fig. 2. A fixed number of certain sightings $S = 5$, and no uncertain sightings, over a fixed time interval (0,100). The time of the last sighting t_n is varying.

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Table 2. Sighting data from Burgman, Grimson & Ferson (1995). All sightings are assumed to be true. Each record represents an independent sighting

Monachus tropicalis		*Mustela nigripes*		*Leporillus conditor*		*Leporillus Apicalis*	
Date	Records	Date	Records	Date	Records	Date	Records
1915	1	1972	4	1835	–	1835	–
1922	1	1973	6	1844	1	1853	1
1932	1	1974	2	1857	1	1857	1
1948	1	1975	3	1879	1	1872	1
1952	1	1976	3	1896	1	1873	1
		1977	1	1897	1	1903	1
		1979	1	1907	2	1929	1
		1981	2	1920	2	1933	2
		1982	3	1921	2		
		1983	1	1930	1		
		1984	2	1933	1		
				1938	1		
				1986	1		
t_0	S	t_0	S	t_0	S	t_0	S
1915	4	1972	10	1835	12	1835	7

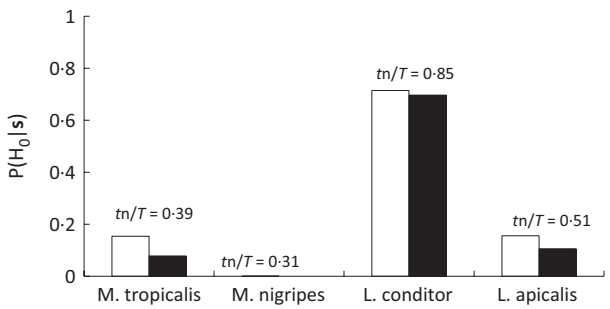

Fig. 3. Comparing methods when only certain sightings are included: the model in this paper (black bar) was applied to four cases with certain sightings only to allow a comparison with Solow's 1993 equation (white bar).

each other. Nonetheless, it is clear that all approaches are likely to be sensitive to the prior. Note that the data for *T. rufolavatus* include a much higher proportion of uncertain sightings than the data for *P. caribbaea*. However, the estimate for the probability of extinction for the latter diverges more than the former when the uncertain sightings are included. The probability that *A. pelzelni* is extant increases when the last and uncertain sighting is included. This would be expected since it is fairly recent. This probability increases further slightly when the quality of this sighting is included (R_α = 0.4 - 0.8). We conclude that there are no general principles with regard to including uncertain sightings.

The records for *L. conditor* include a period of 48 years between 1938 and the last sighting in 1986. If the sighting in 1986 was judged to be uncertain, the probability of being extant reduces drastically from 0·697 to 0·025, demonstrating the critical distinction between certain and uncertain records. Uncertain sightings can be further classified into photographs, observations by experts, etc. Nevertheless, our results indicate that in most cases, further classification may increase the estimation that the species is extant, but does not drastically alter our perception.

Discussion

When uncertain sightings are not included, the method is consistent with existing methods. Most real sighting records are composed of at least some uncertain observations. Discriminating between certain and uncertain sightings can have an important effect of the inferences drawn from observation data. When uncertain sightings are excluded, there may be a considerable difference in the estimate of the probability that a species is extant. It is unclear whether this difference makes inferring extinction either more or less likely. Furthermore, treating an uncertain observation as certain can drastically and falsely increase the estimated probability that a species is extant. In either case, the results could lead to poor decisions and the ineffective allocation of scarce conservation resources.

The innovation in this method is that it handles uncertain sightings throughout the observation period appropriately. The example applications illustrate that using both certain and uncertain sightings, and classing them as such, leads to substantial improvements when inferring whether a species is extinct. The examples also highlight results are sensitive to the prior, as expected with Bayesian methods.

The method allows uncertain sightings to be further classed into a number of different observation types, each with a unique false-positive rate. However, our results indicate that this further classification does not drastically change the probability that a species is extant.

The method does not allow for multiple sightings within the chosen (uniform) time interval. If the data are essentially continuous, then forcing the data into discrete

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Table 3. Sighting data from Birdlife International with probability that the record is true. Each record represents an independent sighting

Tachybaptus rufolavatus		*Pterodroma caribbaea*		*Aplonis pelzelni*	
Prior probability π = 0·9		Prior probability π = 0·825		Prior probability π = 0·36	
Date	Probability true R_α	Date	Probability true R_α	Date	Probability true R_α
1929	1	1789	0·4–0·8	1930	1
1947	0·1–0·4	1829	1	1995	1
1960	1	1847	0·4–0·8	2008	0·4–0·8
1963	1	1866	1		
1969	1	1879	1		
1970	0·1–0·4	1891	0·8–0·9		
1971	0·1–0·4				
1972	0·6–0·8				
1982	0·6–0·8				
1985	0·6–0·8				
1986	0·1–0·4				
1988	0·1–0·4				
t_0	S	t_0	S	t_0	S
1929	3	1789	3	1930	1

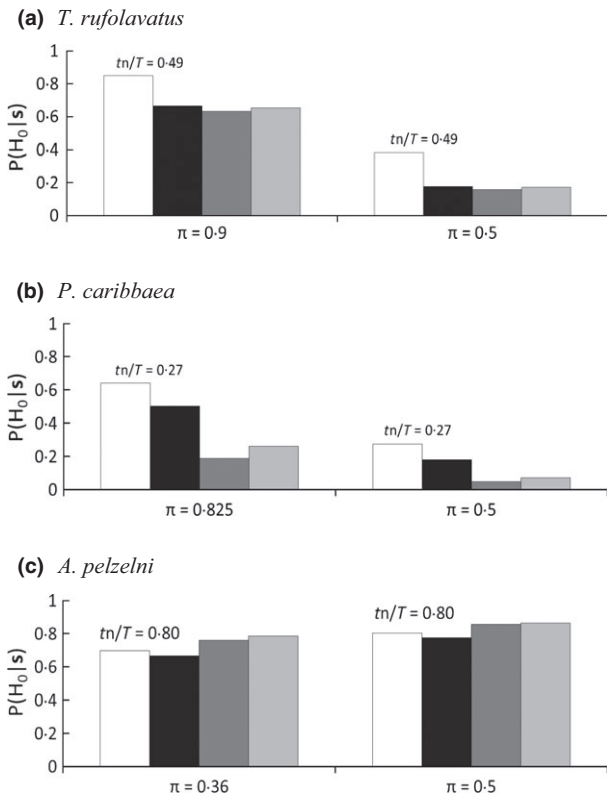

Fig. 4. We applied (i) Solow's 1993 equation to the sighting record with uncertain sightings omitted (white bar). Our model was applied in three ways: (ii) uncertain sightings omitted (black bar); (iii) uncertain sightings were included and grouped together (dark grey bar); (iv) uncertain sightings were included and grouped according to the probability that there were true sightings (light grey bar). The bars on the left used priors provided with the data, and the bars on the right used an unbiased prior.

classes throws away some information. The continuous time version of these models would be more appropriate. However, in many real data sets, observations are essentially discrete because observers provide approximate information (i.e. collection dates that refer to a year, a season or a month). In other instances, observations are not independent because the same person made them on the same or adjacent days, during a single expedition or collecting trip. For a charismatic species such as the ivory-billed woodpecker, one false sighting can lead to others, even in different areas. In such circumstances (where sightings are not independent), using time intervals will mean the data better approximate the underlying independence assumptions in the models since these dependent sightings would be treated as one independent sighting. Burgman, Grimson & Ferson (1995) used this assumption in their application of Solow's 2003 formula. When the multiple sightings are independent from each other, the time interval can be made arbitrarily narrow such that the method approaches the continuous case. Time is a surrogate for survey effort. If a direct measure of effort is available, then the method could be adapted to reflect this measure McCarthy (1997).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. The OpenBugs code for certain and uncertain sightings.

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